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DISTRIBUTIONAL AND PHYLOGENETIC STUDIES ON INDIAN FOSSIL MAMMALS. V

THE CLASSIFICATION AND THE PHYLOGENY OF THE GIRAFFIDAE

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INTRODUCTION

During the later portions of Tertiary times northern India was a great center for the adaptive radiation of the Giraffidae. In the Siwalik deposits of Upper Miocene, Pliocene, and Pleistocene age there is a considerable assemblage of fossil giraffes of varied form, and a study of these Siwalik giraffes throws a great deal of light on the problem of the evolution and the classification of the Giraffidae. A recent review of the fossil giraffes in the Siwalik collection of The American Museum of Natural History has suggested to the present author certain considerations regarding the classification and the phylogeny of the Giraffidae. Some of the questions having to do with the evolution and the classification of this family of artiodactyls will be discussed below.

PREVIOUS CLASSIFICATIONS OF THE GIRAFFIDAE

Some of the more important classification schemes for the Giraffidae are those of Murie (1871), Rütimeyer (1881), Lydekker (1882), von Zittel (revised edition, 1925), Pilgrim (1911), Abel (1919), Bohlin (1927), and Matthew (1929).

MURIE, 1871

In 1871 Dr. James Murie published a paper in the Geological Magazine entitled, 'On the Systematic Position of the *Sivatherium giganteum* of Falconer and Cautley,' in which he discussed the relationships of *Sivatherium* to *Bramatherium* and to other artiodactyls. Basing his conclusions on the development of the horn cores, Murie was led to believe that *Sivatherium* and *Bramatherium* are closely related to the Antilocapridae and to the saiga antelope. He stipulated that the connections between *Sivatherium* and the modern giraffe are of minor importance. Although Murie did not outline a classification for the fossil Giraffidae, he did present a sort of phylogenetic diagram in which he showed *Sivatherium* as being directly related to *Bramatherium*, to the saiga and to the

pronghorn antelope. He interposed the Antilocapridae and the Cervidae between *Sivatherium* and *Giraffa*.

RÜTIMEYER, 1881

Rütimeyer, in his 'Natürliche Geschichte der Hirsche,' published in 1881, failed to realize the relationships existing between the large Siwalik giraffes and the modern giraffe, He placed *Giraffa* among the Cervina, as closely related to the elk. *Helladotherium* from Pikermi was considered as being related to the giraffe, and consequently it was placed with the giraffe among the deer. *Sivatherium*, *Bramatherium*, and *Vishnutherium* from the Siwaliks were assigned to a position among the antelopes, contiguous to the *Damilis* group of South Africa.

LYDEKKER, 1882

It remained for Lydekker to show, in his large monograph on the Siwalik Camelopardalidae published in 1882, that the Siwalik genera, *Sivatherium*, *Hydaspitherium*, *Bramatherium*, etc., are true giraffes, directly related to the modern *Giraffa* and to such fossil forms as *Helladotherium* from Pikermi. Lydekker's realization that these several fossil forms are true giraffes, and that they should be combined with the modern giraffe in one family, is a distinct advance over the views of previous authors.

Lydekker did not divide the Camelopardalidae, as he called it, into lesser groups or subfamilies, but he did arrange the seven genera which he considered as constituting the family in a certain "order of their relationship to one another, indicating a gradual diminution in the length of the limbs and of the neck from the giraffe to the sivathere." Lydekker's arrangement was as follows.

Camelopardalis = *Giraffa*
Orasius
Vishnutherium
Helladotherium
Hydaspitherium
Bramatherium
Sivatherium

This arrangement is valid in that it indicates the relationships of *Orasius* to *Giraffa* and it groups the large giraffids together. Lydekker considered the Camelopardalidae as most closely related to the Cervidae.

VON ZITTEL (revised edition, 1925)

The English translation of von Zittel's 'Textbook of Palaeontology,' published in 1925, includes the Giraffinae and the Sivatheriinae as two

separate subfamilies among the family Cervicornia. The arrangement is as follows.

Family Cervicornia
Subfamily 1.—Moschinae
2.—Cervulinae
3.—Cervinae
4.—Protoceratinae
5.—Giraffinae
6.—Sivatheriinae

According to this classification the genera constituting the two subfamilies are as follows.

Giraffinae
Helladotherium
Palaeotragus
Samotherium
Camelopardalis
Sivatheriinae
Sivatherium
Bramatherium
Hydaspitherium

PILGRIM, 1911

In 1911, Dr. Pilgrim published a memoir entitled 'The Fossil Giraffidae of India.' Although this work was directly concerned only with the Siwalik giraffes, it contained a supplementary consideration of the evolution of the Giraffidae. On page 29 of the publication under consideration there is a phylogenetic diagram of the Giraffidae which classifies the family in the following manner.

GIRAFFIDAE

Palaeotraginae
Palaeotragus
Samotherium
Alcicephalus
Okapia
Indratherium
Libytherium
Helladotheriinae
Helladotherium
Vishnutherium
Giraffokeryx

Progiraffinae
Progiraffa
Giraffinae
Giraffa
Orasius
Sivatheriinae
Sivatherium
Hydaspitherium
Bramatherium
Urmiatherium (placed here rather than in the Bovidae)

This classification is marked by the multiplication of subfamilies, of which one, the Progiraffinae, is founded on rather scanty material, and another, the Helladotheriinae, consists of genera that might very well be placed within two different but well-established groups, the Palaeotraginae and the Sivatheriinae. This will be discussed more fully below.

ABEL, 1919

Abel's classification of the Giraffidae, published in 1919 in his 'Stämme der Wirbeltiere,' is essentially the same as that of von Zittel. He divides the family into two subfamilies, the Giraffinae and the Sivatheriinae.

BOHLIN, 1927

In 1927 Birger Bohlin published an elaborate monograph, 'Die Familie Giraffidae,' a very thorough study of the giraffes, with the fossil material collected by the Swedish expeditions in North China serving as its basis. His classification of the family is given below.

GIRAFFIDAE

Palaeotraginae	**Okapiinae**
Palaeotragus	*Okapia*
Giraffokeryx	**Sivatheriinae**
Achtiaria	*Sivatherium*
Samotherium	*Indratherium*
Alcicephalus	*Bramatherium*
Chersonotherium	*Hydaspitherium*
Shanshitherium	*Helladotherium*
Giraffinae	*Griquatherium*
Giraffa	*Vishnutherium*
Honanotherium	*Libytherium*
Orasius	[**Progiraffinae**]
	[*Progiraffa*]

Bohlin's classification is the most comprehensive and perhaps the best of all the proposed schemes of giraffid taxonomy. His creation of a separate subfamily for the okapi may be disputed; a discussion of this question will be offered below.

MATTHEW, 1929

Dr. Matthew, in his 'Critical Observations upon Siwalik Mammals,' pointed out the desirability of including *Okapia* among the Palaeotraginae, thereby making three subfamilies of the Giraffidae instead of four

(exclusive of the "Progiraffinae"). Matthew's classification is given below.

GIRAFFIDAE

Palaeotraginae	**Giraffinae**
Palaeotragus	*Giraffa*
Samotherium	*Orasius*
Giraffokeryx	*Honanotherium*
Okapia	

Sivatheriinae

Sivatherium+*Indratherium*
Helladotherium+*Bramatherium*
Hydaspitherium

THE RELATIONSHIPS OF *Okapia*

A careful consideration of the problem of a classification of the Giraffidae will demonstrate the validity of Dr. Matthew's views as to the inclusion of *Okapia* in the Palaeotraginae. Bohlin's separation of the okapi into a distinct subfamily is seemingly a flaw in his otherwise admirable classification of this group of artiodactyls. It would seem as if he has placed too much emphasis on minute, and for the most part unimportant characters, and in doing this he has disregarded the great preponderance of characters that typify *Okapia* as a truly primitive palaeotragine. *Okapia* is, in all of its essential characters, a structurally primitive Miocene giraffe (more primitive than *Palaeotragus* or *Samotherium*) that has persisted on to the present day in a region conducive to the continuation of such an early form.

Bohlin has separated the okapi from the Palaeotraginae because:

1.—The frontals are narrow in the modern form, as compared to the fossil species.

2.—The horns are placed in a slightly different position in *Okapia* from the positions of the horns in *Palaeotragus* or *Samotherium*.

3.—The frontals in the okapi tend to develop pneumatic sinuses within them, whereas the sinuses are not pronounced in *Palaeotragus* and related genera.

4.—There are minor differences in the dentition; there is no outer cingulum on DM^2 in the okapi, whereas in *Palaeotragus* and *Samotherium* this cingulum is present.

5.—The skeleton of the okapi differs in small details, especially those of proportions, from the skeleton of *Palaeotragus*.

These are differences of minor importance. Now let us look at *Okapia* and the fossil Palaeotraginae for the purpose of making comparisons between major anatomical characters.

The skull of *Okapia* is in most respects more primitive than the skull of the fossil Palaeotraginae. The canine-premolar diastema of the mandible is much shorter in the okapi than it is in the fossil forms, showing that the modern species has retained a short muzzle, a primitive and a diagnostic heritage character. In the okapi the frontals are narrow, which is to be expected in a relatively primitive artiodactyl. In *Palaeotragus* the frontals are wide, and this may be considered as an habitus character, subsequent to the narrow frontal region. An examination of various groups of ungulates will show that the skull tends to elongate first, after which it widens, if the tendency to widen exists at all. That is, elongation precedes lateral expansion. Consequently we may expect a primitive giraffid, such as the okapi, to have a narrower frontal region than a more advanced form in which the cranium has broadened out.

Of course, as Bohlin has shown, the frontals of the okapi contain rather large sinus cavities, which are lacking in *Palaeotragus* and *Samotherium*. It may be quite probable that the development of the frontal sinuses in the okapi are of a secondary nature, and that they have been acquired more or less independently in the long period of time that has elapsed between the Miocene and the present day. But this is no reason for excluding the okapi from a place as a relatively primitive palaeotragine. It is a primitive genus that has developed certain specialized characters during the passage of geologic time.

In *Okapia* the horn cores are rather small, whereas in *Palaeotrabus* they are much larger. Thus we may regard the okapi as more primitive in its horn development than is *Palaeotrabus*. Of course, one might argue that the small horns in the okapi are degenerate structures, secondarily reduced from larger horns, but in answer to this argument it might be said that the horn cores in the okapi have retained a primitive position over the orbit, and this would favor their being truly primitive structures. This primitive position of the horn cores is retained in *Palaeotrabus*, but in *Samotherium* the horn cores have shifted somewhat to the rear, due to the elongation of the skull.

In *Okapia* the dentition is very brachyodont—a primitive character. In *Palaeotragus* and *Samotherium* the teeth are considerably higher than is the case in the modern genus, showing that the fossil forms are relatively advanced in the stage of their phylogenetic development.

The skeleton of the okapi is certainly primitive. It shows little of the elongation of the limbs, or of transverse growth of the skull and skeletal elements that appear in the more advanced Giraffidae.

Therefore, considering *Okapia* with regard to its major anatomical characters, without special emphasis on small, single features, we see that it is a very primitive giraffid, more primitive even than *Palaeotragus*, and that it is a satisfactory structural ancestor for the Palaeotraginae. It has the diagnostic heritage characters of the Palaeotraginae, but in this persistent genus very few of the advanced habitus characters that characterize the fossil genera have been developed.

The Relationships of *Giraffokeryx;* Other Problems

The genus *Giraffokeryx* was created by Pilgrim in 1910, on the basis of upper and lower cheek teeth. In 1911, this author, in his monograph of the Siwalik Giraffidae, placed *Giraffokeryx* along with *Helladotherium* and *Vishnutherium* in a separate subfamily, the Helladotheriinae. Bohlin, in 1927, went to the other extreme and reduced the genus *Giraffokeryx* to synonymy with *Palaeotragus*, including it, naturally, in the subfamily Palaeotraginae. Both of these authors were founding their conclusions on the evidence of teeth alone.

An almost complete skull of *Giraffokeryx* in the American Museum gives much evidence that helps to solve the question of the taxonomic position of the genus. This skull has recently been described by Colbert (1933), and it is shown to be essentially a *Palaeotragus*-type with an extra pair of horn cores on the frontals. Therefore the genus *Giraffokeryx* properly belongs in the subfamily Palaeotraginae, where it was placed by Bohlin and later by Matthew. It is, however, a separate genus, quite distinct from *Palaeotragus*, but closely related to it.

Bohlin and Matthew have both given conclusive evidence to show that the genera *Hellodotherium* and *Vishnutherium* should be included in one subfamily with *Sivatherium*, *Hydaspitherium*, *Bramatherium*, etc. Consequently Pilgrim's subfamily Helladotheriinae would seem to be unnecessary.

The subfamily Progiraffinae, created by Pilgrim in 1911, is based on rather insufficient material. The genus *Progiraffa* (*Propalaeomeryx*) may be perfectly valid, and it may deserve separation from the other Giraffidae as a distinct subfamily, but at the present time the material is not plentiful enough to prove this. Until further material is discovered it would seem best to include this genus tentatively among the Palaeotraginae.

The reader is referred to Matthew's 'Critical Observations upon Siwalik Mammals,' published in 1929, for illuminating notes and discussions concerning the Siwalik Giraffidae.

With the foregoing discussion in mind we may now attempt a new classification scheme for the Giraffidae.

Classification of the Giraffidae

Giraffidae

Large, ruminating artiodactyls, with heavy, rugose cheek teeth. The skull may or may not have horn cores, but if they are present they show a great variety of development. Bones of cranial roof pneumatic. Lateral metapodials and digits atrophied.

Palaeotraginae

Primitive, medium sized giraffids, having as a rule one pair of supraorbital frontal horn cores. There may be a second pair of horn cores at the anterior extremities of the frontals. Horn cores in the form of simple tines, well developed in the males, feebly developed or absent in the females. Skull usually elongated.

Cheek teeth brachyodont, with moderately coarse sculpture of the enamel. Limbs and neck slightly elongated.

Palaeotragus Gaudry, 1861

Palaeotragus rouenii Gaudry—Generic type. Pontian, Lower Pliocene; Pikermi, Samos.

Palaeotragus parvus (Weithofer). Synonym of *P. rouenii.*

Palaeotragus vetustus (Wagner). Synonym of *P. rouenii.*

Palaeotragus microdon (Koken). Pontian, Lower Pliocene; China.

Palaeotragus coelophrys (Rodler and Weithofer). Pontian, Lower Pliocene; Maragha, China.

Palaeotragus decipiens Bohlin. Pontian, Lower Pliocene; China.

Palaeotragus quadricornis Bohlin. Pontian, Lower Pliocene; Samos, Maragha, China.

Palaeotragus expectans (Borissiak). Sarmatian, Upper Miocene; Sebastopol.

Achtiaria Borissiak, 1914

Synonym of *Palaeotragus*

Achtiaria expectans (Borissiak)—Generic type.

Giraffokeryx Pilgrim, 1910

Giraffokeryx punjabiensis Pilgrim—Generic type. Lower and Middle Siwaliks, Lower Pliocene; India.

OKAPIA Lankester, 1901

Okapia johnstoni (Sclater)—Generic type. Recent; Africa.

SAMOTHERIUM Forsyth Major, 1888

Samotherium boisseri Forsyth Major—Generic type. Pontian, Lower Pliocene; Samos.

Samotherium neumeyeri (Rodler and Weithofer). Pontian, Lower Pliocene; Maragha, China.

Samotherium sinense (Schlosser). Pontian, Lower Pliocene; China.

Samotherium tafeli (Killgus). Lower Pliocene; China.

Samotherium eminens (Alexejew). Lower Pliocene; Odessa.

ALCICEPHALUS Rodler and Weithofer, 1890

Synonym of *Samotherium*

Alcicephalus neumeyeri Rodler and Weithofer—Generic type.

CHERSONOTHERIUM Alexejew, 1916

Synonym of *Samotherium*

Chersonotherium eminens Alexejew—Generic type.

SHANSHITHERIUM Killgus, 1922

Synonym of *Samotherium*

Shanshitherium tafeli Killgus.—Generic type.

Provisionally Placed in the Palaeotraginae

PROPALAEOMERYX Lydekker, 1883

Propalaeomeryx sivalensis Lydekker—Generic type. Lower Siwaliks (?), Lower Pliocene; India.

PROGIRAFFA Pilgrim, 1908

Progiraffa exigua Pilgrim—Generic type. Bugti beds, Lower Miocene; Sind.

Giraffinae

Large giraffids with a moderately brachycephalic skull. Horns variously developed, being located on the parietals and the frontals. In *Giraffa* a single median horn is also present, located on the nasals. Horn cores rounded or flattened on the ends, and covered with hair. Skull roof with highly developed sinus cavities.

Cheek teeth brachyodont, with heavily rugose enamel. Limbs and neck greatly elongated.

GIRAFFA Brisson, 1756

Giraffa camelopardalis (Linnaeus)—Generic type. Recent; Africa.

Giraffa sivalensis (Falconer and Cautley). Upper Siwaliks, Pleistocene; India.

Giraffa affinis (Falconer and Cautley). Synonym of *G. sivalensis*.

Giraffa punjabiensis Pilgrim. Middle Siwaliks, Pliocene; India.
Giraffa priscilla Matthew. Lower Siwaliks, Lower Pliocene; India.
Giraffa nebrascensis Matthew and Barbour. Pleistocene; Nebraska. (This genus?)

ORASIUS Oken, 1816

Orasius atticus (Gaudry and Lartet). Pontian, Lower Pliocene; Pikermi.
Orasius eximius Wagner. Synonym of *O. atticus*.
Orasius speciosus (Wagner). Synonym of *O. atticus*.

(The reader should refer to Matthew, 1929, p. 546, for a discussion of this genus. The name "*Orasius*" is used here only in a provisional way.)

HONANOTHERIUM Bohlin, 1927

Honanotherium schlosseri (Pilgrim)—Generic type. Pliocene; China.

Sivatheriinae

Gigantic giraffids, with large, heavy brachycephalic skulls. Horn cores variously developed, being of frontal and parietal origin. Skull roof with large sinus cavities.

Cheek teeth moderately hypsodont, with heavily rugose enamel. Limbs not elongated but very heavy. Body heavy.

SIVATHERIUM Falconer and Cautley, 1835

Sivatherium giganteum Falconer and Cautley—Generic type. Upper Siwaliks, Pleistocene; India.

INDRATHERIUM Pilgrim, 1910

Synonym of *Sivatherium*
Indratherium majori Pilgrim—Generic type. Upper Siwaliks, Pleistocene; India.

BRAMATHERIUM Falconer, 1845

Bramatherium perimense Falconer—Generic type. Middle Siwaliks, Pliocene; Perim Island.

HYDASPITHERIUM Lydekker, 1878

Hydaspitherium megacephalum Lydekker—Generic type. Middle Siwaliks, Pliocene; India.
Hydaspitherium grande Lydekker. Middle Siwaliks, Pliocene; India.
Hydaspitherium magnum Pilgrim. Middle Siwaliks, Pliocene; India.
Hydaspitherium birmanicum Pilgrim. Irrawaddy beds, Pliocene; Burma.

VISHNUTHERIUM Lydekker, 1876

Vishnutherium iravaticum Lydekker—Generic type. Irrawaddy beds, Pliocene; Burma.

HELLADOTHERIUM Gaudry, 1860

Helladotherium duvernoyi GAUDRY—Generic type. Pontian, Lower Pliocene; Pikermi, Samos.

Helladotherium gaudryi DE MECQUENEM. Pontian, Lower Pliocene; Maragha.

GRIQUATHERIUM Haughton, 1922

Griquatherium cingulatum Haughton—Generic type. Pleistocene; South Africa.

Of Uncertain Position

LIBYTHERIUM Pomel, 1893

Libytherium maurusicum Pomel—Generic type. Pliocene; North Africa.

RELATIONSHIPS OF THE GIRAFFIDAE TO THE PROTOCERATIDAE

The Protoceratidae of North America have been linked to the Giraffidae by some authors, on the basis of certain resemblances between the members of the two groups. Schlosser, especially, would derive the Giraffidae directly from the Protoceratidae. Both Bohlin and Matthew have shown, however, that the resemblances between the Protoceratidae and the Giraffidae are due to convergence, and that these two families are really separated from each other by differences of basic importance.

There are certain resemblances in the teeth between the Protoceratidae and the more primitive Giraffidae, resemblances that may be attributed to primitive heritage characters carried over from a common Eocene ancestor. The skull resemblances, especially in the development of numerous pairs of horn cores in several genera of these two families, are due entirely to a convergence in evolutionary trends. Both the Protoceratidae and the Giraffidae produced horn cores anterior to and posterior to the orbits. But these horn cores are derived from different skull elements in the two groups. This is well illustrated by the anterior horn cores, which are of premaxillary origin in the Protoceratidae, and of frontal origin in the Giraffidae.

Dr. Matthew[1] made the following remarks with regard to the origin of the Giraffidae and the relation of this family to the North American Protoceratidae.

"The family appears to be a group of specialized survivals of the Middle Miocene Palaeomerycinae, of which *Dromomeryx*, the American genus, is the only one known from complete skulls and associated skeletons. The horns of *Dromomeryx* are of giraffoid type, long, straight, probably skin-covered, nondeciduous, supra-orbital, and with a basal

[1]Matthew, W. D. 1929. Bull. Amer. Mus. Nat. Hist., LVI, p. 545.

wing that suggests the later complications in the sivatheriines. Teeth quite close to *Palaeotragus* and *Giraffokeryx*.

"Schlosser would derive giraffes from Protoceratinae, but this does not seem to be a tenable phylogeny. The protoceratines are an early specialized group of Traguloidea, with no approach to the Pecora in foot characters. The Giraffidae are true Pecora, fully developed as such in the feet, and nearly related through Palaeomerycinae to the primitive Cervidae (cf. *Eumeryx* of the Stampian Oligocene of Mongolia)."

Phylogeny of the Giraffidae

In the accompanying chart (Fig. 1), an attempt has been made to represent the phylogeny of the Giraffidae in a graphic form. On this chart the geologic distribution of the family is represented along the vertical axis, whereas the geographical extent is shown along the horizontal axis. The three subfamilies of the Giraffidae are shown by parallel shading; the Palaeotraginae being represented by vertical lines, the Giraffinae by oblique lines and the Sivatheriinae by horizontal lines. The primitive Palaeomerycidae, from which the Giraffidae might have been derived, are shown also. Certain genera, such as *Propalaeomeryx*, *Griquatherium*, etc. are omitted from this chart.

It will be seen that the Giraffidae is a family of Miocene derivation, having its origin in the Holarctic region. It is characterized by the rapidity of evolution of its subfamilies and genera; all of the great variety of giraffid form and structure having been established since late Miocene times.

The evolutionary development of the group took place in Europe and Asia. The okapi and the giraffe, the one a persistent primitive genus and the other a genus that specialized early in the evolutionary history of the group, migrated to Africa from the Holarctic center of origin. The survival of these two forms in Africa, far from the center of origin of the family, is what might be expected. Matthew has shown, in his 'Climate and Evolution,' that persistent primitive species migrate away from the center of origin and their place is taken by more specialized forms. Or, to put it in a different way, the primitive and inadaptive species are pushed out by the specialized, adaptive species, so they must needs find refuge in peripheral regions, far distant from their place of origin.

With regard to the rapidity of evolution among the Giraffidae and the center of ultimate origin for the group, I take the liberty once more of quoting from Dr. Matthew.[1]

[1]Matthew, W. D. 1929. *Op. cit.*, pp. 553–555.

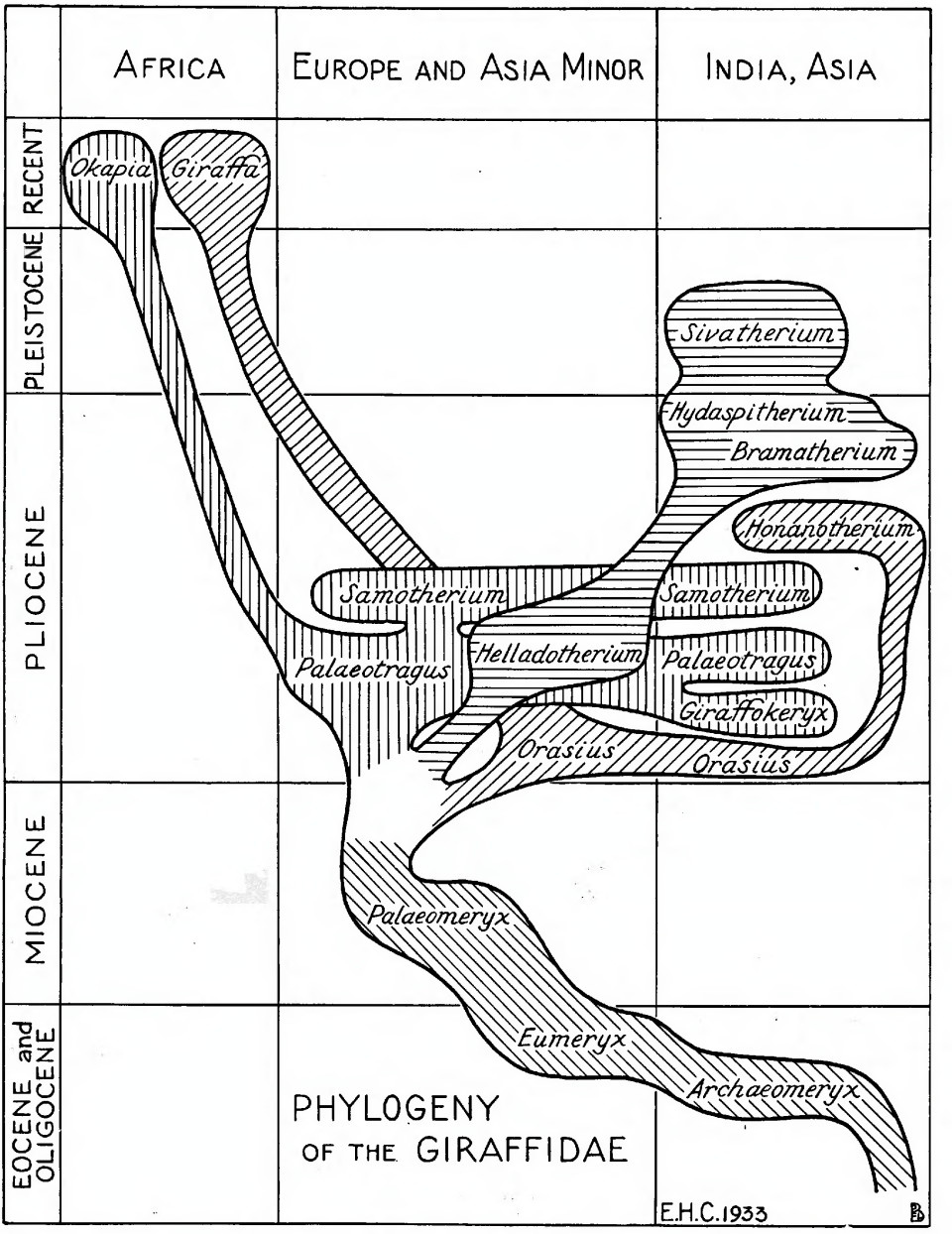

Fig. 1. The Phylogeny of the Giraffidae. The stratigraphic occurrences of the genera are represented by their vertical arrangement, and their geographic distribution is shown by their horizontal arrangement. Lines of shading represent taxonomic divisions, as follows.

GIRAFFIDAE	
Palaeotraginae	vertical lines
Sivatheriinae	horizontal lines
Giraffinae	oblique lines
PALAEOMERYCIDAE	oblique lines

"I do not in fact think that the Giraffidae are an old family, or that any of them are very wide apart in spite of the diversity of skull structure. The lack of diversity in tooth structure is, to my mind, not due so much to the lack of change in the teeth as to the rapidity of change in the skull, and the whole family derives from late Miocene palaeomerycines, an antiquity decidedly less than most mammalian families."

"All in all, I cannot see anything more primitive in the Chinji Giraffidae than Pikermi can show, and I see no reason for hunting a separate evolution center for the giraffes in Africa when the Holarctic Miocene palaeomerycines afford a perfectly good ancestral group."

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